Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles[1,2,3]

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ABSTRACT: The objectives of this experiment were to determine the extent of variation in proteolysis, sarcomere length, and collagen content among pork muscles and the association of those factors with tenderness variation among muscles at 1 d postmortem. Twenty-three white composite barrows were slaughtered and carcasses (66 kg) were chilled at 0°C for 24 h. At 1 d postmortem, the longissimus lumborum, biceps femoris, semimembranosus, semitendinosus, and triceps brachii, long head were dissected from one side of each carcass and frozen. Trained sensory panelists evaluated tenderness, amount of connective tissue, juiciness, and pork flavor intensity of grilled (70°C) chops on 8-point scales. Raw chops were used for total collagen content, sarcomere length, and the extent of desmin proteolysis. Tenderness ratings were highest ($P < .05$) for semitendinosus (7.2) and triceps brachii (7.1), followed by longissimus lumborum (6.4) and semimembranosus (5.7) and were lowest ($P < .05$) for biceps femorus (4.0). The simple correlations between longissimus lumborum tenderness and the tenderness of other muscles were .54 (semimembranosus), .34 (semitendinosus), .36 (triceps branchii), and .17 (biceps femorus). Total collagen was highest ($P < .05$) for biceps femorus (7.1 mg/g muscle), followed by triceps branchii (6.0 mg/g) and semitendinosus (5.3 mg/g), and lowest for semimembranosus (4.5 mg/g) and longissimus lumborum (4.1 mg/g). Sarcomere length was longest ($P < .05$) for semitendinosus (2.5 μm) and triceps branchii (2.4 μm), followed by semimembranosus (1.8 μm), longissimus lumborum (1.8 μm), and biceps femorus (1.7 μm). Proteolysis of desmin was greatest ($P < .05$) in longissimus lumborum (39.3%), followed by semimembranosus (21.0%) and biceps femoris (18.5%), then semitendinosus (.2%) and triceps brachii (.2%). Multiple linear regression using total collagen, sarcomere length, and proteolysis accounted for 57% of the variation in tenderness rating among all samples. Piecewise linear regression was used to account for the interaction of sarcomere length with proteolysis and collagen. This analysis accounted for 72% of the variation in tenderness rating. Variation in collagen, proteolysis, and sarcomere length and the degree of their interaction with one another determine the tenderness of individual muscles.

Key Words: Collagen, Muscle, Pork, Proteolysis, Sarcomere Length, Tenderness

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Introduction

Historically, pork longissimus has been considered to be relatively tender (DeVol et al., 1988); thus, little pork tenderness research has been conducted. However, available data contradict the assumption that pork is uniformly tender. It has been reported that there was significant animal-to-animal variation in pork tenderness (Davis et al., 1975; DeVol et al., 1988). Furthermore, recent emphasis in the United States on selection for increased lean growth in pork has been associated with unfavorable changes in the rate of postmortem pH decline, postrigor calpastatin activity, and tenderness (Huff-Lonergan et al., 1997, 1998). Therefore, there is growing concern among pork industry leaders that selection for increased pork carcass leanness may have a negative impact on tenderness (Meisinger and Miller, 1998). In agreement with this concern, Cameron (1990) found that with selection for increased carcass lean weight, the meat becomes less tasty, less juicy, less tender, and lower in overall acceptability.

The sources of variation in beef longissimus tenderness have been studied extensively (for review see Koohmaraie, 1992, 1996). However, pigs are slaughtered

[1]The authors express their gratitude to P. Ekeren, K. Mihm, and P. Tammen for technical assistance and to M. Bierman for secretarial assistance.

[2]Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

[3]Anti-desmin (clone D3) was developed by D. A. Fischman and obtained from the Developmental Studies Hybridoma Bank maintained by Univ. of Iowa, Dept. of Biol. Sci., Iowa City, IA 52242, under contract N01-HD-7-3263 from the NICHD.

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Received May 26, 1999.

Accepted October 6, 1999.

at a younger physiological age, have a smaller carcass mass, a greater, more uniform fat thickness, a faster metabolic rate (Etherington et al., 1987), and lower calpastatin activity (Ouali and Talmant, 1990; Koohmaraie et al., 1991). These differences could lead to differences in chilling rate, pH decline, rigor shortening, rate and extent of proteolysis, and quality and quantity of connective tissue, all of which could affect tenderness. However, there are limited data on pork tenderness, particularly for muscles other than the longissimus. Thus, the objectives of this experiment were to determine the extent of variation in proteolysis, sarcomere length, and collagen content among and within pork muscles and the association of those factors with tenderness variation among and within muscles at 1 d postmortem.

Materials and Methods

Samples

The Roman L. Hruska U.S. Meat Animal Research Center Animal Care and Use Committee approved the use and treatment of animals in this experiment according to guidelines established by the USDA. Twenty-three white composite barrows were humanely slaughtered and skinned carcasses (66 kg) were chilled at 0°C for 24 h. Muscles were sampled at 1 d postmortem to maximize variation in tenderness (Wheeler and Koohmaraie, 1994). At 1 d postmortem, the longissimus lumborum, biceps femoris, semimembranosus, semitendinosus, and triceps brachii, long head were dissected from one side of each carcass, vacuum-packaged and frozen at –20°C. Frozen muscles were cut into chops 2.54 cm thick. Longissimus chops were cut beginning 2 cm anterior to the ilium. Chops from all other muscles were cut from the thickest portion of the muscle. Longissimus chops 4, 6, 9, and 11 were assigned to sensory evaluation. Longissimus chop 3 was assigned to sarcomere length, Western blotting, and collagen analyses. For each of the other four muscles, four chops were cut. Chops 1, 2, and 4 were assigned to sensory evaluation and chop 3 was assigned to other laboratory analyses.

Immunoblotting

Extraction, electrophoresis, Western blotting, and quantification of desmin were conducted as described by Wheeler and Koohmaraie (1999) except that gels were loaded with 15 μg of protein per lane. Samples for reference standards were obtained from each muscle of one carcass within 30 min postmortem. The data reported are the percentages of the at-death desmin that was degraded.

Sarcomere Length

Three raw muscle cubes, one each from lateral, central, and medial locations within transverse sections (chop 3) of each muscle, were removed and fixed according to Koolmees et al. (1986). From each cube, sarcomere length of eight fiber samples was determined (24 total measurements per observation) by helium neon laser diffraction (model 05-LHR-021, Melles Griot, Carlesbad, CA) as described by Cross et al. (1981). The remainder of chop 3 was trimmed of epimysium and powdered in liquid nitrogen for collagen determination.

Total Collagen Content

Total collagen was estimated from hydroxyproline quantification similar to the ion-exchange method described by Avery et al. (1996). Raw muscle was powdered in liquid nitrogen. Powdered sample (1.5 g) was dried at 110°C for 30 min. Dried sample was ground using a mortar and pestle and hydrolyzed in 50 mL of 6 *N* HCl. Samples were purged with nitrogen for 10 min, then heated for 20 h at 110°C. Cooled samples (23°C) were filtered (Whatman 54) and brought to 100 mL with water. A 50-mL aliquot was evaporated to dryness, rehydrated with water, then evaporated to dryness again. Samples were rehydrated in sodium diluent (product 239440: .27 *N* sodium salt and .01 *N* phenol; Beckman Instruments, San Ramon, CA) and brought to 50 mL. An aliquot was filtered (.2 μm Gelman Supor 200) and a 500-μL aliquot was mixed with 28 μL of 2.5 μ*M* cysteic acid as the internal standard. Amino acids were separated by ion-exchange chromatography (Spectra Physics HPLC system) using a 3- × 250-mm column and 10-μm cation exchange Na form resin (Pickering #1193250). Calculations were based on a standard curve using serial dilutions of *trans*-4-hydroxy-L-proline and adjusted for internal standard variation. Hydroxyproline was converted to collagen by multiplying by 7.25 (Woessner, 1961; Goll et al., 1963). Data are expressed as milligrams of collagen per gram of raw muscle.

Cooking

Chops for trained descriptive attribute panel evaluation were thawed (5°C) until an internal temperature of 5°C was reached then were cooked with a belt grill (model TBG-60 Magigrill, MagiKitch'n Inc., Quakertown, PA). Belt grill settings (top heat = 163°C, bottom heat = 163°C, preheat = 149°C, height [gap between the platens] = 21.6 mm, cook time = 5.7 min) were designed to achieve a final internal temperature of 70°C for chops 2.54 cm thick (Wheeler et al., 1998). After the chops exited the belt grill, a needle thermocouple was inserted into the geometric center of the chop and postcooking temperature rise was monitored with a hand-held thermometer (Cole-Parmer, Vernon Hills, IL). The maximum temperature, which was reached approximately 2 min after the chop exited the belt grill, was recorded as the final cooked internal temperature.

Trained Sensory Evaluation

Chops were evaluated immediately after cooking by an eight-member trained descriptive attribute sensory

panel as described by Wheeler et al. (1998), except pork flavor intensity (1 = bland, 8 = extremely intense) was evaluated instead of beef flavor intensity.

Statistical Analyses

Data were analyzed by mixed model analysis of variance with PROC MIXED of SAS (1997) for a split-plot design (Steel and Torrie, 1980). The whole-plot treatment was the random effect of animal. The split-plot treatment was muscle (longissimus lumborum, biceps femoris, semimembranosus, semitendinosus, and triceps brachii). Mean separation for significant ($P < .05$) muscle effects was accomplished by the PDIFF option (a pairwise *t*-test) of the least squares procedures (SAS, 1997). Multiple linear regression was used to predict tenderness rating using collagen, sarcomere length, and proteolysis. Piecewise linear regression was used to account for the effects of the interaction of collagen and proteolysis with sarcomere length on tenderness rating (Neter et al., 1989).

Results and Discussion

Semitendinosus and triceps brachii received the highest ($P < .05$) tenderness ratings, followed by longissimus, then semimembranosus, and biceps femoris received the lowest ($P < .05$) mean tenderness rating (Table 1). Longissimus had the highest SD for tenderness rating and the largest CV, although semimembranosus and biceps femoris had similar CV. Variability in semitendinosus and triceps brachii tenderness ratings was relatively low. Batcher and Dawson (1960) reported differences in tenderness ratings among pork muscles, although they did not evaluate the triceps brachii, and they found similar tenderness ratings for semimembranosus and biceps femoris. Nold et al. (1997) reported higher tenderness ratings (7 d postmortem) for longissimus than for semitendinosus in pigs slaughtered at 100 kg live weight, but the opposite was found in pigs slaughtered at 110 kg. McKeith et al. (1985) reported that at 1 d postmortem, of the five muscles in the present study, beef longissimus had the highest tenderness rating and the other four were all similar. Other studies have compared Warner-Bratzler shear force among muscles; however, it has been shown that Warner-Bratzler shear force does not accurately measure tenderness differences among muscles (Harris and Shorthose, 1988; Shackelford et al., 1995). Furthermore, care must be exercised when comparing the tenderness of longissimus to other muscles. This relationship is not constant. It varies because tenderness is more variable in longissimus than in most other muscles (Shackelford et al., 1995). Thus, depending on the tenderness level of the longissimus, it may be more or less tender than many of the other muscles.

The highest simple correlations among muscles for tenderness rating were between semimembranosus and either longissimus or biceps femoris (Table 2). Correlations among other muscle combinations were moderate to low. The correlations of other muscles to longissimus for tenderness had little agreement with those reported for beef by Shackelford et al. (1995). In those data (for the same muscles used in the present study), triceps brachii was most highly correlated (.56), followed by biceps femoris (.43), semimembranosus (.26), and semitendinosus (.13). The differences among these studies may be due to inherent differences between species or due to the lack of aging time in the pork. However, the differences could reflect the lower repeatability of tenderness in muscles other than the longissimus (Shackelford et al., 1997).

Ratings for amount of connective tissue (Table 1) were highest ($P < .05$) for semitendinosus, triceps brachii, and longissimus (least amount of connective tissue), intermediate for semimembranosus, and lowest ($P < .05$) for biceps femoris (most connective tissue). The results of Shackelford et al. (1995) were similar, except that semitendinosus was rated to have more connective tissue than triceps brachii and longissimus, but still less than semimembranosus. McKeith et al. (1985) reported sensory ratings indicating longissimus had the lowest amount of connective tissue, followed by semitendinosus and triceps brachii, then semimembranosus; biceps femoris had the most connective tissue.

Ratings for juiciness, pork flavor intensity, and off-flavor were slightly higher ($P < .05$) for semitendinosus and triceps brachii than for longissimus, semimembranosus, and biceps femoris (Table 1). The differences in juiciness, flavor intensity, and off-flavor may have been due to autocorrelation with tenderness ratings. Nold et al. (1997) found no difference in juiciness ratings between longissimus and semitendinosus. In beef, Shackelford et al. (1995) and McKeith et al. (1985) found that triceps brachii, longissimus, and biceps femoris were more juicy than semitendinosus and semimembranosus.

It is generally accepted that connective tissue and myofibrillar components (including sarcomere length and extent of postmortem proteolysis) are the main effectors of meat tenderness (for review see Harris and Shorthose, 1988). However, to our knowledge, no one has published data that include all three factors in multiple muscles to determine the relative contribution of each factor to the tenderness of each muscle. We have known that muscles vary greatly in sarcomere length (Herring et al., 1965a) and connective tissue content (Ramsbottom et al., 1945). However, little is known about the extent of postmortem proteolysis in most muscles. Thus, it has not been possible to determine how these three factors interact to affect tenderness in different muscles.

Desmin degradation ranged from −14 to 81% (Table 3). Clearly, no values below zero should be obtained. We believe the negative values were the result of inherent variation in the protocol in samples with practically zero degradation (see Wheeler and Koohmaraie [1999]for an example of a Western blot from the protocol used). The percentage of desmin that was degraded was greatest ($P < .05$) for longissimus, slightly lower for semimembra-

Table 1. Descriptive statistics for trained sensory panel traits among muscles

Trait and muscle	Mean	SD	Minimum	Maximum	CV
Tenderness[a]					
Semitendinosus	7.2[f]	.45	6.5	7.9	6.3
Triceps brachii	7.1[f]	.38	6.4	7.7	5.4
Longissimus	6.4[g]	1.08	3.4	7.5	16.9
Semimembranosus	5.7[h]	.82	3.1	6.8	14.4
Biceps femoris	4.0[i]	.62	2.8	5.1	15.5
Amount of connective tissue[b]					
Semitendinosus	7.6[f]	.21	7.2	7.9	2.8
Triceps brachii	7.5[f]	.26	7.1	7.9	3.5
Longissimus	7.2[f]	.58	5.5	7.8	8.1
Semimembranosus	6.7[g]	.43	5.4	7.3	6.4
Biceps femoris	5.4[h]	.49	4.1	6.1	9.1
Juiciness[c]					
Semitendinosus	5.9[f]	.35	5.3	6.6	5.9
Triceps brachii	5.8[f]	.25	5.4	6.3	4.3
Longissimus	5.3[g]	.28	4.6	5.8	5.3
Semimembranosus	5.4[g]	.29	4.6	5.8	5.4
Biceps femoris	5.2[g]	.25	4.8	5.6	4.8
Pork flavor intensity[d]					
Semitendinosus	4.9[g]	.40	4.1	5.6	8.2
Triceps brachii	4.8[g]	.41	4.0	5.4	8.5
Longissimus	5.2[f]	.34	4.6	5.8	6.5
Semimembranosus	5.1[f]	.39	4.0	5.7	7.6
Biceps femoris	5.2[f]	.32	4.3	5.6	6.2
Off-flavor[e]					
Semitendinosus	2.9[g]	.26	2.2	3.3	9.0
Triceps brachii	2.9[g]	.24	2.4	3.4	8.3
Longissimus	3.3[f]	.24	2.7	3.6	7.3
Semimembranosus	3.2[f]	.27	2.5	3.7	8.4
Biceps femoris	3.1[f]	.25	2.6	3.6	8.1

[a]1 = extremely tough, 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.
[b]1 = abundant, 5 = slight, 6 = traces, 8 = none.
[c]1 = extremely dry, 5 = slightly juicy, 8 = extremely juicy.
[d]1 = bland, 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.
[e]1 = intense, 2 = moderate, 3 = slight, 4 = none.
[f,g,h,i]Means in a column within a trait lacking a common superscript differ ($P < .05$).

nosus and biceps femoris, and near zero for semitendinosus and triceps brachii (Table 3). Although muscles were sampled at d 1 postmortem in order to maximize tenderness variation, longissimus, semimembranosus, and biceps femoris had a relatively large range in the amount of desmin proteolysis. Based on beef data, we would expect additional aging time to result in increased desmin degradation. However, in pork, tenderization progresses at a faster rate (Dransfield et al., 1981; Etherington et al., 1987). Koohmaraie et al. (1991) reported that desmin was degraded at a much higher rate in pork longissimus than in beef or lamb longissimus, but some additional desmin degradation and shear force reduction occurred after 7 and 14 d postmortem in pork. Iversen et al. (1995) reported only a slight increase in 30-kDa protein and no change in Warner-Bratzler shear force in pork longissimus aged 7 d relative to 1 d postmortem. To our knowledge, there have been no published data on direct measures of postmortem proteolysis among muscles in pork. In beef, Taylor et al. (1995) reported that at 1 d postmortem little desmin degradation had occurred in either biceps femoris or semitendinosus, but that by 6 d postmortem 10 and 75% of desmin was degraded in biceps femoris and semimembranosus, respectively.

Table 2. Simple correlation coefficients among muscles for tenderness rating

Muscle	SM	BF	ST	TB[a]
Longissimus	.54**	.17	.34	.36
Semimembranosus (SM)		.53**	−.22	.34
Biceps femoris (BF)			−.37	.20
Semitendinosus (ST)				.07

[a]TB = triceps brachii.
**$P < .01$.

The variation in sarcomere length among beef muscles (Herring et al., 1965a) and its effect on meat tenderness (Locker, 1960) have been established. However, given the faster rate of rigor development, these differences may not be the same for pork muscles. Sarcomere length was much longer ($P < .05$) in semitendinosus and triceps brachii than in the other three muscles (Table 3). Longissimus sarcomere length was not different ($P > .05$) from either semimembranosus or biceps femoris sarcomere

Table 3. Descriptive statistics for traits associated with variation in tenderness among muscles

Trait and muscle	Mean	SD	Minimum	Maximum	CV
Desmin, % degraded					
Semitendinosus	.2[c]	5.2	–11.4	8.2	2,600
Triceps brachii	.2[c]	9.1	–13.8	9.8	4,550
Longissimus	39.3[a]	25.4	–12.6	81.3	64.6
Semimembranosus	21.0[b]	12.9	.2	43.6	61.4
Biceps femoris	18.5[b]	15.4	–.8	54.3	83.2
Sarcomere length, μm					
Semitendinosus	2.45[a]	.14	2.1	2.8	5.6
Triceps brachii	2.44[a]	.17	2.0	2.7	7.1
Longissimus	1.78[bc]	.10	1.5	2.0	5.6
Semimembranosus	1.83[b]	.06	1.6	2.0	3.3
Biceps femoris	1.74[c]	.10	1.5	1.9	5.9
Collagen, mg/g					
Semitendinosus	5.3[c]	1.0	3.7	7.4	18.9
Triceps brachii	6.0[b]	1.5	4.4	9.8	25.0
Longissimus	4.1[d]	.7	2.8	6.0	17.1
Semimembranosus	4.5[d]	.7	3.2	5.7	15.6
Biceps femoris	7.1[a]	1.1	5.2	8.9	15.5

[a,b,c]Means in a column within a trait comparing muscles lacking a common superscript differ ($P < .05$).

length. All semitendinosus and triceps brachii samples had sarcomere lengths of 2.0 μm or longer, whereas all samples from the other three muscles had sarcomere lengths of 2.0 μm or shorter. Herring et al. (1965b) reported that bovine semitendinosus from control carcasses chilled at 1°C and excised at 2 d postmortem had a sarcomere length of 2.6 μm (similar to our pork data). In a random sample of 120 pork carcasses from a large commercial pork processor, DeVol et al. (1988) reported that in longissimus, sarcomere length averaged 1.83 μm and ranged from 1.66 to 2.00 μm. Our results on sarcomere length agree with those of DeVol et al. (1988) for pork, as well as with previous results in beef (Herring et al., 1965a,b; McKeith et al., 1985) and lamb (Hostetler et al., 1972; Quarrier et al., 1972). Thus, it seems from the present study that if sarcomere length could be extended to at least 2.0 μm, the muscle would be tender regardless of collagen content or proteolysis (Figure 1). However, data from Hostetler et al. (1972) do not support that hypothesis. The inconsistent effects of increasing sarcomere length (up to > 3 μm) on shear force (Hostetler et al., 1972) may indicate the high degree of interaction among sarcomere length, proteolysis, and connective tissue on tenderness differences among muscles.

Collagen concentration was highest ($P < .05$) in biceps femoris, followed by triceps brachii and semitendinosus, and was lowest ($P < .05$) in semimembranosus and longissimus (Table 3). Triceps brachii was most variable in collagen concentration. DeVol et al. (1988) also reported that longissimus collagen concentration averaged 3.95 mg/g wet tissue weight and ranged from 2.20 to 6.16 mg/g. For each muscle, our estimates of collagen concentration were lower than published estimates for beef (Cross et al., 1973; McKeith et al., 1985).

The percentage of desmin that was degraded was significantly correlated, ranging from weak to moderate, with all traits except tenderness and connective tissue ratings when all muscles were included (Table 4). Sarcomere length had the strongest correlation with desmin degradation. This likely resulted from the long sarcomeres and minimal desmin degradation in semitendinosus and triceps brachii, rather than being a direct association of the two traits. Wheeler and Koohmaraie (1999) have shown desmin and troponin-T proteolysis were independent of sarcomere length. Collagen content was weakly, but significantly, correlated with tenderness, connective tissue, flavor intensity, and off-flavor ratings.

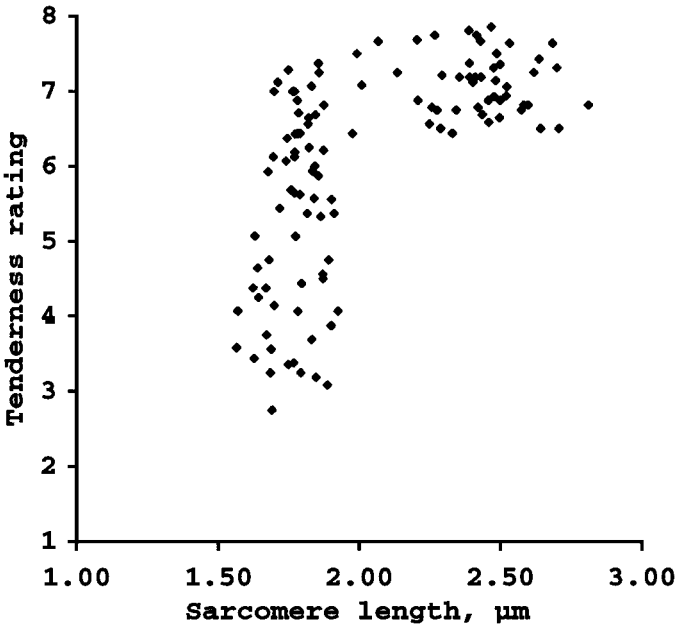

Figure 1. A plot of tenderness rating and sarcomere length for all five muscles.

Table 4. Simple correlation coefficients for various traits within and across all muscles

Trait	Collagen, mg/g	Sarcomere length, μm	Tenderness[a]	Connective tissue[b]	Juiciness[c]	Flavor intensity[d]	Off-flavor[e]
				All muscles			
Desmin, % degraded[f]	–.23*	–.61**	–.16	–.21	–.40**	.38**	.48**
Collagen, mg/g	—	.04	–.34**	–.38**	–.09	–.22*	–.31**
Sarcomere length, μm	—	—	.64**	.62**	.64**	–.38**	–.50**
Tenderness[a]	—	—	—	.94**	.60**	–.18	–.22*
				Semitendinosus			
Desmin, % degraded[f]	.17	.12	–.07	–.08	–.44*	–.07	–.02
Collagen, mg/g	–	–.14	.10	.00	–.23	–.30	–.35
Sarcomere length, μm	—	—	–.40	–.10	–.48*	.06	.20
Tenderness[a]	—	—	—	.43*	.40	.16	.06
				Triceps brachii			
Desmin, % degraded[f]	–.03	–.02	.24	.08	.23	–.07	–.22
Collagen, mg/g	—	–.24	.11	.01	–.26	–.23	–.18
Sarcomere length, μm	—	—	.09	.02	.09	–.11	–.17
Tenderness[a]	—	—	—	.67**	.41*	–.12	–.05
				Longissimus			
Desmin, % degraded[f]	.01	–.42*	–.08	–.33	–.15	.41	.51*
Collagen, mg/g	—	–.25	–.21	–.04	–.47*	–.21	–.19
Sarcomere length, μm	—	—	.67**	.56**	.35	–.12	–.31
Tenderness[a]	—	—	—	.84**	.60**	.27	.16
				Semimembranosus			
Desmin, % degraded[f]	.09	.00	.51*	.39	.30	.28	.12
Collagen, mg/g	—	–.07	–.26	–.05	–.47*	–.05	–.32
Sarcomere length, μm	—	—	–.21	–.06	.06	–.19	–.06
Tenderness[a]	—	—	—	.85**	.23	.09	.05
				Biceps femoris			
Desmin, % degraded[f]	.03	–.28	.61**	.24	.34	.07	.11
Collagen, mg/g	—	–.08	.02	–.05	–.04	–.25	–.29
Sarcomere length, μm	—	—	–.19	–.02	–.04	.12	.20
Tenderness[a]	—	—	—	.73**	.15	–.01	.20

[a]1 = extremely tough, 8 = extremely tender.
[b]1 = abundant, 8 = none.
[c]1 = extremely dry, 8 = extremely juicy.
[d]1 = extremely bland, 8 = extremely intense.
[e]1 = intense, 4 = none.
[f]Percentage of at-death desmin that was degraded.
*$P < .05$.
**$P < .01$.

Sarcomere length was moderately correlated with all traits except collagen content. The higher correlation between sarcomere length and tenderness rating was likely due to the long sarcomeres and high tenderness ratings for the semitendinosus and triceps brachii. Correlations of other traits to sarcomere length may have been due to autocorrelation with tenderness rating. Tenderness rating was strongly correlated with the rating for sensory panel connective tissue amount but was only weakly correlated with an objective measurement of collagen content.

Within individual muscles, fewer significant correlations occurred than with all muscles combined. Tenderness rating was significantly correlated with connective tissue amount rating in all muscles. In semitendinosus, juiciness rating was significantly correlated with desmin degradation and sarcomere length. In triceps brachii, tenderness rating also was significantly correlated with juiciness ratings. The longissimus had more significant correlations among traits than other muscles. In the longissimus, desmin degradation was significantly correlated with sarcomere length and off-flavor rating. Tenderness rating also was significantly correlated with juiciness rating. Collagen content was significantly correlated with juiciness rating, and sarcomere length was significantly correlated with tenderness and connective tissue amount ratings. In both semimembranosus and biceps femoris, tenderness rating also was significantly correlated with desmin degradation. In addition, collagen content was significantly correlated with juiciness rating in the semimembranosus.

The ability of desmin degradation, sarcomere length, and collagen content to predict tenderness rating singularly and combined within and across all muscles was highly variable (Table 5). Because there was little variation in the tenderness ratings of semitendinosus and triceps brachii, there was little opportunity to predict tenderness variation in those muscles. Sarcomere length

accounted for 16% of the variation in tenderness in semitendinosus. All three variables combined also accounted for 16% of the variation in tenderness of semitendinosus. Variation in tenderness ratings of triceps brachii could not be explained by variation in these three traits. Variation in tenderness rating was most predictable in longissimus. Within longissimus, sarcomere length accounted for 44% of the variation, whereas all three traits combined explained 49% of the variation in tenderness. It is likely that desmin degradation would explain a much higher proportion of variation in longissimus tenderness if a longer aging time had been used. Desmin degradation explained 26 and 38% of the variation in tenderness of semimembranosus and biceps femoris, respectively. With all three traits combined, 41 and 38% of the variation in tenderness was explained in semimembranosus and biceps femoris, respectively. In beef, we have reported that tenderness measurements were more repeatable in longissimus than in other muscles due to a greater amount of animal-to-animal variation (Shackelford et al., 1997; Wheeler et al., 1997), and, thus, longissimus tenderness should be more predictable. Furthermore, given the repeatability estimates of beef longissimus tenderness measurements of .70 to .90 (Wheeler et al., 1997), we would expect to be able to explain, at most, 50 to 80% of the variation in longissimus tenderness. Repeatability estimates for beef semitendinosus and biceps femoris of .60 and .50, respectively (Shackelford et al., 1997), indicate we would not expect to be able to explain more than 36 and 25% of the variation in tenderness of these muscles. In addition, coefficients of determination are further limited by the repeatabilities of the measurements of the independent variables.

When all muscles were combined, sarcomere length explained 40% of the variation in tenderness. Using multiple linear regression, desmin degradation, sarcomere length, and collagen explained 57% of the variation in tenderness of all muscles combined. However, as indicated in Figure 1, when all muscles were combined, the relationship between sarcomere length and tenderness was not linear, and therefore piecewise linear regression was used. Sarcomere length was treated as a class variable (< 2 and > 2 μm) and interacted with collagen and proteolysis (desmin degradation). For samples with sarcomere length > 2 μm, neither collagen content nor desmin degradation was related to tenderness rating. For samples with sarcomere length < 2 μm, both collagen content and desmin degradation were related to tenderness rating ($P < .001$). This model explained 72% of the variation in tenderness rating (Figure 2).

Table 5. Coefficients of determination for predicting tenderness rating within and across pork muscles

Muscle	Desmin, % degraded[a]	Sarcomere length, μm	Collagen, mg/g	All three variables
Semitendinosus	.01	.16	.01	.16
Triceps brachii	.06	.01	.01	.08
Longissimus	.01	.44	.04	.49
Semimembranosus	.26	.04	.07	.41
Biceps femoris	.38	.04	.00	.38
All muscles	.03	.40	.11	.57

[a]Percentage of at-death desmin that was degraded.

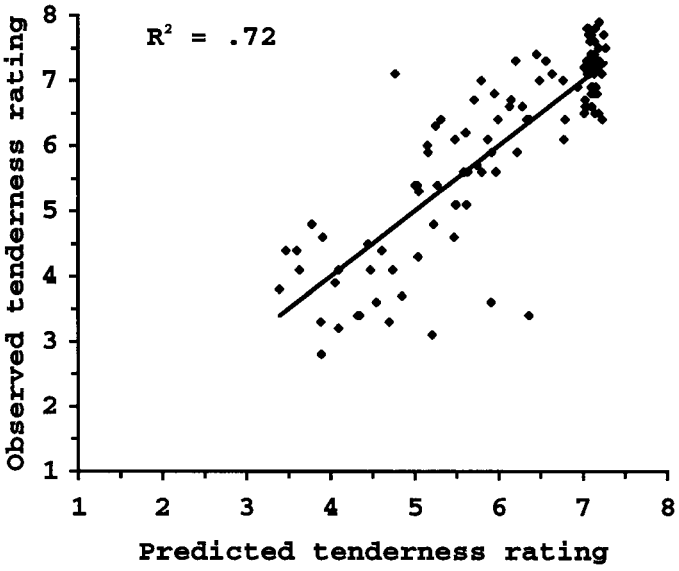

Figure 2. A plot of predicted and observed tenderness ratings for all five muscles combined. Using piecewise regression, tenderness ratings were predicted as follows: If sarcomere length < 2 μm then: y = 7.2 + (–.46 × collagen) + (.019 × desmin). All coefficients were significant ($P < .001$) and the standard errors of the estimates were .288, .047, and .004, respectively. If sarcomere length > 2 μm then: y = 7.2 + (–.018 × collagen) + (.007 × desmin). The coefficients for collagen and desmin were not significant ($P > .61$) and the standard errors of the estimates were .288, .052, and .014, respectively.

Due to long sarcomeres, semitendinosus and triceps brachii were tender despite high collagen content and low proteolysis. Due to shorter sarcomeres, longissimus was less tender than semitendinosus and triceps brachii, despite less collagen and greater proteolysis. Due to lower proteolysis, semimembranosus was less tender than longissimus, but semimembranosus was more tender than biceps femoris due to lower collagen. Sarcomere length, proteolysis, collagen content, and the degree of their interaction varies among muscles; thus, the relative contributions of these factors to tenderness variation is muscle-specific.

Implications

These data indicate the importance of sarcomere length to tenderness in unaged muscle. The relative contribution of sarcomere length, collagen content, and proteolysis to tenderness variation varies among muscles and would likely change after aging. One should not expect to explain much more than 72% of the variation in tenderness due to the limitations of sampling and measurement error compounded by measurement of

multiple traits and the low repeatability of tenderness measurements in some muscles. Sarcomere length, proteolysis, and collagen content must be known in order to explain differences among muscles in tenderness and, subsequently, to devise strategies to eliminate tenderness deficiencies of specific muscles.

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